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Traits of dominant species and soil properties co-regulate soil microbial T communities across land restoration types in a subtropical plateau region of Southwest China

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Keywords: Plant functional traits, Soil microbial community, Mass-ratio hypothesis, Soil properties

Abstract

Soil microbial community is essential for maintaining and improving ecosystem functioning in ecological re-storation practice and is intimately linked with the plant community. However, little is known on how soil microbial communities respond to the functional characteristics of plant communities. Here we investigated the changes in plant community functional attributes, soil properties, and soil microbial community characteristics of four land restoration (vegetation) types in a subtropical plateau region. The relative contributions of soil abiotic properties and plant community functional attributes to variation in microbial community composition and function were then assessed. We found that plant community attributes, soil properties, and the soil microbial communities differed significantly among land restoration types, and the plant functional traits of dominant species and soil properties jointly determined soil microbial community structure and functions. Specifically, soil microbial community structure was significantly linked to the community-weighted mean (CWM) of plant functional traits, soil water content, and soil organic carbon. Soil

microbial carbon-metabolic functions were tightly correlated with the CWM of leaf dry matter content, specific leaf area, and specific root length. Variance partitioning also revealed that the CWM of plant functional traits and soil variables co-operatively explained 67% and 64% variation in soil microbial community structure and carbon-metabolic functions. Meanwhile, significant correlations were found between variation in microbial community composition and carbon-metabolic functions. In conclusion, our observations demonstrate that soil microbial community characteristics were governed by dominant species in plant communities across land restoration types, mainly due to differences in plant functional traits and soil resource driven by plant traits.

1. Introduction

Biodiversity has been considered the key determinant of changes in ecosystem processes and functions (Hooper et al., 2005). Some studies have reported that the species diversity of an aboveground community may affect the soil functions via changes in soil biological and physicochemical properties (Landesman et al., 2014; Lladó et al., 2018). However, an increasing focus of research is devoted to the functional characteristics of organisms, exploring how changes in functional diversity influence soil functions and their response to environmental change (Bardgett, 2017; Faucon et al., 2017; Grigulis et al., 2013; Lavorel et al., 2013). Further, trait-based approaches are being used to predict how changes in vegetation composition influence soil properties and processes (Bardgett, 2017; De Deyn et al., 2008; Grigulis et al., 2013). Soil microbial community, as a major driver of soil biogeochemical cycles, soil formation, and ecosystem resilience to the external environment, is important to soil properties and processes (Khelifa et al., 2017; Wardle et al., 2004). However, the effects of functional plant traits and their diversity on soil microbial communities are far from being fully understood.

Changes in soil microbial community composition are not only influenced by soil physicochemical factors such as pH, soil organic carbon (SOC), and nutrient availability (Landesman et al., 2014; Lladó et al., 2018) but also by plant properties such as plant community type, plant-microbial interactions, and plant functional traits (Bauhus and Paré, 1998; de Vries et al., 2012; Pei et al., 2016). Scheibe et al. (2015) demonstrated that tree species identity and site conditions were more important factors in determining the soil microbial community structure than tree species diversity. It has been proposed that plant leaf economics spectrum could provide a framework for understanding how vegetation composition influences variation in soil microbial communities (Wardle et al., 2004). The general idea is that plant species with a higher specific leaf area (SLA) and a lower leaf dry matter content (LDMC) can shape the bacteria-dominated soil microbial communities. In contrast, plant species with low SLA promote the growth of fungi relative to bacteria (Orwin et al., 2010; Wardle et al., 2004). However, these studies measured only plant attributes on the species scale and did not consider functional characteristics on the community scale. Therefore, we do not understand how soil microbial communities respond to changes in the functional diversity of the plant community.

Functional diversity of plant community describes the distribution of species in functional trait space and is hypothesized as being beneficial for ecosystem processes and functions (Mason et al., 2005). At the community scale, the community-weighted means (CWM) of some functional traits (e.g., SLA, LDMC, or plant height), which describes the dominant functional trait value of a community and is closely related to the mass ratio hypothesis, can respond to environmental change and affect soil biological processes and nutrient cycling (Garnier et al., 2004). The mass ratio hypothesis proposes that ecosystem functioning is primarily determined by the functional traits of the dominant species and is frequently used to quantify the functional characteristics of plant communities (Lavorel et al., 2008). Simultaneously, soil microbial community may be modified by soil physicochemical properties that are induced by changes in community functional attributes (De Deyn et al., 2008; Orwin et al.,

2010). Some studies of plant-soil interactions have confirmed that soil properties (e.g., pH, soil moisture, soil organic carbon) play an important role in the interactions between plant species and soil microbial communities (De Deyn et al., 2009; Harrison and Bardgett, 2010). Therefore, it is plausible that plant community functional attributes and their effect on soil properties (such as soil texture and nutrient resources) cooperatively shape the structure and functions of soil microbial communities.

Concerns over the continuing loss of biodiversity and the associated decline of ecosystem functions have triggered numerous studies aiming at developing more sustainable ecological protection and restoration practices (Faucon et al., 2017). Many studies suggest that, compared with plant species richness, plant functional traits and functional diversity metrics can be used to evaluate functional responses to re-storation projects (D'Astous et al., 2013; Laughlin, 2014; Zirbel et al., 2017). In the subtropical plateau region of southwest China, different land restoration types including naturally recover and establishing plantations have been widely adopted for maintaining soil fertility and controlling soil and water loss. For example, plantation forest with Eucalyptus or Pinus species is considered as one of the main forms of land restoration due to their attributes of fast growth and industrial production of wood, oil, and fuel. At the same time, natural regeneration has also proved to be another effective approach to land restoration in this area (Fu et al., 2018). Although previous studies have shown that different vegetation restoration methods influence plant community composition, soil nutrients, and ecosystem functions (e.g. water and soil conservation) (Fu et al., 2009, 2018; Hou et al., 2010), little is known on how soil microbial communities respond to the functional characteristics of plant communities in this region.

In this study we investigated changes of soil microbial community composition and carbon-metabolic function in different land restoration types using phospholipid fatty acid analysis (PLFA) and community-level physiological profiles (CLPP), respectively, and then evaluated the relative effects of plant community attributes and soil physicochemical properties on soil microbial communities. We hypothesized that (1) soil microbial community composition and carbon-metabolic functions differ between the different land restoration types; (2) soil microbial communities are significantly driven mainly by changes in the plant community-weighted means of functional traits the functional traits and soil physicochemical properties.

2. Material and methods

2.1. Study area

The study area is located at Jiulongdian catchment (257.6 km²) in Mouding County (25°24'09" N, 101°28'18" E), mid-Yunnan, SW China. The average annual rainfall in the area, which lies in the subtropical monsoon climate zone, is 846 mm, and the rainy season lasts from May to October each year. The average annual temperature is 16 °C. The soil of the area is Cambisols (according to FAO/UNESCO classifications). The original vegetation in this region was a subtropical evergreen broad-leaved forest, most of which was utilized as coppices for fuel-wood or pastures. Since the 1980s, some of these have been planted by fast-growing *Pinus yunnanensis* after deforestation. Other remnant cop-pices and pastures were abandoned and formed different secondary stands after natural regeneration.

Currently, this area represents sections of different vegetation including secondary shrubland (SL), coniferous forest (CF), semi-natural forest (SNF), and natural secondary forest (NSF) (Tang et al., 2010). These four land restoration types are described as follows: (1) SL, the land has been closed for at least 15 years since the last domestic live-stock grazing and repeated cutting; (2) CF, the man-made plantation is dominated by the coniferous species *P. yunnanensis* with a history of aerial

planting on abandoned lands followed by the closing of the land for reforestation; (3) SNF, mixed needle-broad leaved forest dominated by *P. yunnanensis* and *Keteleeria evelyniana* with a history of clear-cut-ting followed by a period of approximately 45 years of forest reservation; and (4) NSF, dominated by *Cyclobalanopsis glaucoles* and *K. evelyniana* and reserved without any interruption for a period of approximately 55 years.

2.2. Investigation and sampling procedures

In July and August 2018, we selected three representative sites with four vegetation restoration types in this catchment. The sites are located at Samachang (25°14'35" N, 101°27'12" E, app. 2050 m.a.s.l.), Huafoshan (25°18'48" N, 101°25'12" E, app. 2340 m.a.s.l.), and Ximiji (25°15'23" N, 101°25'23" E, app. 2010 m.a.s.l.). The distance between the sites is greater than 2.5 km to reduce the effects of spatial auto-correlation. In each site, we established a representative 10 × 10 m plot for each vegetation restoration type. The plot of one vegetation type is more than 200 m apart from another vegetation type on the same site. All 12 plots belonged to the same climatic and soil zones and have a similar slope direction (20–25° west of north) and gradient (15–17°). Plant species diversity and community functional characteristics in each plot were firstly calculated based on the investigation of plant community structure and estimation of plant functional traits for each species. Second, ten soil cores from 0 to 10 cm were taken at random locations in each plot. These cores were pooled and sieved (2 mm mesh) to eliminate rocks and stones. Each mixed sample was divided into two subsamples: one was used to analyze basic soil physicochemical properties; the other was freeze-dried to analyze the soil microbial community composition and functions. Additionally, another three un-disturbed soil samples were collected by metal cylinders to measure soil water content (SWC).

2.3. Plant community properties

For each plot, the abundance of a given species was determined based on the basal area or the estimation of percent cover for plants < 1.5 cm DBH (details in Fu et al., 2018). In the analyses, a total of 27 species were recorded and used to quantify species diversity (H, Shannon index; R, richness; and E, evenness) and plant community functional attributes. Five important plant functional traits: leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), and specific root length (SRL) were selected because these traits are closely correlated with plant potential relative growth rate, nutrient quality, nutrient acquisition strategy, and productivity (Cornelissen et al., 2003; Vile et al., 2006). These traits were measured based on at least 5 individuals of each species following standardized protocols (Cornelissen et al., 2003), and the mean of each trait for each species was calculated and then used to calculate the community functional attributes. The CWMs were used as the index of functional diversity of plant community, which calculated for each trait and for every plot using the mean species trait values and the species relative abundance (Garnier et al., 2004). The species diversity and all the indices of community functional attributes were calculated using the FDiversity software package (Casanoves et al., 2011).

2.4. Soil physicochemical properties

Soil physicochemical properties including pH, soil water content (SWC), soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) were determined. Soil pH was measured in a 1:2.5 (soil to water ratio) mixture using a glass electrode. The SWC, SOC, TN, and TP were measured using the drying method, the potassium dichromate sulfuric acid oxidation, the semi-micro Kjeldahl, and the phosphomolybdate blue methods, respectively. All procedures for the determination of soil physicochemical indices were based on the methods described in Gregorich and Carter (2007).

2.5. Soil microbial community analysis

The soil microbial community structure and carbon metabolic functions were characterized using PLFAs and CLPPs. The PLFAs were extracted from 4 g of soil with a chloroform: methanol: phosphate buffer mixture (1:2:0.8, v/v/v) following the procedure of Frostegård et al. (Frostegård et al., 1993). The extracted lipids were eluted with chloroform, acetone, and methanol on solid-phase extraction columns to obtain the phospholipids. The phospholipids were then subjected to mild alkaline methanolysis, and the extractions were redissolved in hexane with an internal standard of 19:0. Finally, the samples were analyzed using gas chromatography/mass spectrometry with the following parameters: capillary column (HP-5), He as a carrier gas at a flow rate of 0.8 mL min⁻¹, and an injection volume of 1 µL. The abundance of individual PLFAs was expressed as nanomoles of PLFAs per gram dry soil (nmol/g), and the total PLFAs was calculated as the sum of all PLFAs and used a measure of microbial biomass. The different PLFAs were considered to represent different taxonomic groups: Gram-negative (G-) bacteria were represented by cy17:0, 16:1 ω 7, 18:1 ω 7 and cy19:0 (Zogg et al., 1997); Gram-positive bacteria (G+) were represented by i15:0, a15:0, i16:0, i17:0 and a17:0 (Moore-Kucera and Dick, 2008); fungal biomass was represented by 18:2 ω 6,9 and 18:1 ω 9 (Bååth and Anderson, 2003); actinomycete biomass was represented by 10Me16:0, 10Me17:0 and 10Me18:0 (Moore-Kucera and Dick, 2008); arbuscular mycorrhizal fungi (AMF) were represented by 16:1 ω 5c (Frostegård and Bååth, 1996); and 20:3 ω 6 and 20:4 ω 6 were assumed to represent protozoans (Ringelberg et al., 1997). The structure of the soil microbial community was also characterized using the fungi:bacteria ratio (F:B) and the G+:G- ratio.

The capacity of soil microbial communities to utilize carbon sources was assessed with CLPPs using Biolog EcoPlates (Biolog, Inc., USA). Each EcoPlate contained 31 different carbon sources, which were divided into six groups: carboxylic acids, polymers, carbohydrates, phenolic acids, amino acids, and amines. Soil suspensions were obtained according to the method described by Wu et al. (2013) and were then inoculated into each well. The plates were incubated at 25 °C for 10 days, and

the color development in each well was recorded as the optical density at 590 nm with an automated plate reader at regular 24 h intervals. Finally, the soil microbial activity in each microplate was assessed as the average well color development (AWCD) as follows: $AWCD = \sum ODi / 31$, where ODi is the optical density value in each well.

2.6. Statistical analysis

Plant community characteristics (species diversity and CWM for each trait), soil physicochemical properties, soil microbial community composition and carbon-metabolic functions (PLFAs and CLPPs, re-spectively) under different land restoration types were compared using a one-way ANOVA and an LSD test. We further used non-metric mul-tidimensional scaling (NMDs) based on the Bray-Curtis index to vi-sualize the dissimilarity in soil microbial composition across plots. NMDs is an effective method in community analysis because it does not assume linear distribution of the data (Pei et al., 2016). The significance of the variations in the composition of soil microbial community was tested by PERMANOVA with Bray-Curtis dissimilarities and 999 per-mutations. We did not include the spatial location of the plots in data analyses because spatial autocorrelation is not significant using Mantel test.

To quantify the relative importance of soil properties and plant community attributes for the soil microbial community composition and carbon-metabolic functions. Variance partitioning analysis was applied for all the plots based on redundancy analysis (RDA) to illus-trate the explanatory power of three matrices including soil physico-chemical properties, plant species diversity, and plant functional di-versity (anova.cca function in package vegan). The significance of each explanatory factor was assessed using a permutation test. We further analyzed the correlations between biplot scores from RDA and en-vironmental factors using the functional envfit. In addition, we analyzed the correlations among soil microbial community characteristics, plant community attributes, and soil properties with Spearman correlation. Prior to the above analyses, when the raw data did not meet the nor-mality assumptions, they were log- or sqrt-transformed. The above statistical analyses were

performed in R version 3.4.0 (R Core Team, 2017) using the package vegan (Jari et al., 2013) and SPSS (version 19.0; SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Plant community attributes and soil physicochemical properties

The ANOVA showed that all indices of plant community attributes except species richness were significantly changed under different land restoration types. Shannon index and evenness were significantly lower in CF than in the other three land restoration types (Table 1). For the CWMs, the different traits displayed trait-specific responses to land restoration types. SL and CF had a higher CWM for SLA, LNC, LPC, and SRL. SNF and NSF had a higher CWM for LDMC.

Land restoration types had significant effects on soil physicochemical properties, except pH (Table 1). Specifically, SWC and SOC were higher in NSF and SNF than in SL and CF. In addition, the soils in the NSF had a significantly higher TN and TP than the other plant communities. The correlation analysis revealed that there are strong relationships among SWC and SOC ($P < .01$). In addition, the CWM of SRL was strongly linked to all soil properties except soil pH. Besides of SRL, variation in the CWM for LDMC and LPC were significantly associated with SWC, whereas CWM for LDMC and SLA was tightly correlated with SOC (Table 2).

3.2. Soil microbial community structure and function

Individual PLFA indicator lipids differed in their response to different land restoration types (Table 3). The NMDs analysis of the PLFAs revealed that land restoration type had a significant effect on microbial community structure (Fig. 1A, $P < .001$). The relative abundances of all the microbial groups except actinomycetes and protozoa were significantly higher in NSF and SNF than in SL and CF (Table 3).

The ANOVA showed that the carbon-utilization intensity of all compounds except amines significantly differed across land restoration types (Table 3). The NMDs analysis of the CLPPs revealed that land restoration type had a significant effect on microbial community carbon-metabolic functions (Fig. 1B, $P < .003$). Similarly to PLFA, total metabolic activity (indicated by AWCD) and the utilization intensity of the carbon sources except amines were significantly higher in NSF and SNF than in SL and CF (Table 3).

3.3. Factors determining soil microbial community characteristics

The correlation analysis results showed that all the RDA axes of the microbial PLFAs were significantly linked to the CWM of every trait and the soil properties (SWC and SOC) (Table 4). In addition, the RDA axes of the microbial CLPPs was tightly correlated with species richness and can also be explained by the CWM for LDMC, SLA, and SRL (Table 4). Moreover, we also found a significant correlation between soil micro-bial community composition and carbon-metabolic functions by the permutation test ($P < .05$, results not shown).

Results of variation partitioning showed that plant functional di-versity and soil physicochemical properties cooperatively explained most variation in the soil microbial community composition and function across land restoration types (Fig. 2). The joint explanations by the two factors were 0.67 and 0.64, respectively. Other factors did not significantly explain the variations in soil microbial community struc-ture and function.

Overall, shifts in the soil microbial community composition across land restoration types occurred in parallel with changes in the CWM of traits and soil variables. Changes in soil microbial metabolic functions were primarily associated with the CWMs and soil microbial community structure.

4. Discussion

4.1. Soil microbial community characteristics among land restoration types

Soil microbial community composition significantly differed among the four land restoration types (Fig. 1A, Table 3). The total biomass of the soil microbial community was twice as high for SNF and NSF than for SL and CF (Table 3). Some studies have confirmed that this phenomenon may be attributed to aboveground productivity and litter input because SOC promotes the growth of soil microbes (Gunina et al., 2017; Zhao et al., 2017). In addition, a significant difference for PLFAs was found among land restoration types. With regard to bacterial bio-mass, the greatest abundance of G+ and G- bacteria were found in SNF and NSF, which is consistent with the results of Gunina et al. (2017), who found that there is a greater abundance of G+ and G- bacteria in forest soils than in agricultural soils. The greater abundance of G+ and G- bacteria in NSF and SNF may be linked to the more diverse litter carbon from heterogeneous plant litter inputs (Fierer et al., 2003) and the volume of the rhizosphere due to the increase in plant density (Thoms and Gleixner, 2013), respectively.

The reasons for the greater abundance in fungal PLFAs in SNF and NSF can be attributed to both the replacement of species and changes in the microenvironment. The replacement of species with readily de-composable litter by those with more recalcitrant leaf litter can stimulate the growth of the fungal biomass (Yannikos et al., 2014). Simultaneously, most species in SNF and NSF are strongly ectomycorrhizal or arbuscular-mycorrhizal such as plants of the genera *Cyclobalanopsis*, *Quercus*, *Pinus*, and *Keteleeria* in the study area (Tedersoo and Brundrett, 2017). Moreover, the reduced environmental disturbance in SNF and NSF may also enhance the growth of fungi (Strickland and Rousk, 2010). The increase in actinomycete PLFA content could also be linked to the more recalcitrant leaf litter in SNF and NSF, because actinomycetes may produce enzymes targeting complex and recalcitrant biopolymers (Zhao et al., 2019).

The Biolog EcoPlate data identified potential carbon utilization activities for the soil microbial community and can be used to assess soil microbial metabolic functions (Liu et al., 2010; Zak et al., 1994; Zhao et al., 2019). In our research, the CLPP analyses revealed differences among different

land restoration types and showed that the microbial communities in SNF and NSF have a greater potential for utilization of diverse carbon sources compared with SL and CF (Table 3, Fig. 1B). This phenomenon may indicate that there is higher microbial biomass and diversity in SNF and NSF, and furthermore, a greater proportion of the microbial community may be able to utilize diverse carbon compounds (Liu et al., 2010; Zhao et al., 2019), which also confirmed by the significant correlation between PLFAs and CLPPs.

4.2. Explanatory factors for soil microbial community among land restoration types

We found that the CWMs for plant functional traits are the most important drivers of soil microbial community structure and function (Table 4). The LDMC, as the functional trait for the ratio of structural compounds to the assimilatory issue, represents leaf and litter structural compounds and quality (Cornelissen et al., 2003). The significant positive correlation between the CWM for LDMC and soil microbial community structure and carbon-metabolic functions suggests that an additional carbon source (e.g., cellulose or insoluble sugars) in the litter with higher LDMC improves microbial growth, although some chemically resistant components may decrease the rate of litter decomposition (Pei et al., 2016). This explanation is supported by the clear relationship between CWM-LDMC and SOC. The SLA, LNC, and LPC are the proxies for litter quality and decomposition rate. Higher values of these functional traits represent higher leaf quality and a more rapid litter decomposition rate, which may lead to a decrease in SOC and soil microbial community composition.

Besides aboveground leaf traits, we also found that the CWM for SRL was not only significantly related to all the soil properties but also to soil microbial community composition and function (Tables 2, 4), which suggests that underground SRL plays a critical role in below-ground ecosystem properties and functions, including the soil microbial community. Recent studies have confirmed that the CWM for root traits explains the variation in microbial parameters related to N cycling better than shoot traits (Legay et al., 2014). Root traits are generally regarded as an indicator of plant resource uptake strategies, soil nutrient cycling, and root exudate quantity and quality

(Bardgett et al., 2014; Cornelissen et al., 2003; Vile et al., 2006). Root litter and root exudates are the key sources of soil nutrients and energy for microbes. However, we found a negative relationship between the CWM for SRL and soil microbial community, which suggests that root density or root biomass could play a more important role due to their effects on the quantity of root litter inputs and rhizodeposition (Orwin et al., 2010). Therefore, in future research, more root traits should be examined to explore how roots traits influence the soil microbial community and its impacts on soil ecosystem processes and functions (Bardgett et al., 2014).

Many studies have confirmed that soil characteristics, for example, soil pH, SWC, and soil nutrients, play a significant role in shaping the composition of soil microbial communities (Bååth and Anderson, 2003; Fierer et al., 2009; Lladó et al., 2018; Stark and Firestone, 1995). In the present study, we only found that SWC and SOC are the key factors, probably due to their influence on soil microbial activities and the fluxes of soil nutrients (Brockett et al., 2012; Stark and Firestone, 1995; Zhao et al., 2017). Although some studies have reported soil pH as one of the drivers for soil microbial community composition, we did not find a significant correlation between pH and soil microbial community composition. This may be due to the narrow acidic pH range (4.08–4.26). It is widely recognized that soil nutrients can support and shape the growth and composition of microbial communities (Fierer et al., 2009). It was surprising that soil TN and TP did not play a key role in influencing the soil microbial community in our study. However, we detected significant positive correlations between SOC and the soil microbial community structure. This is consistent with previous studies, which showed that changes in SOC induced by aboveground litter input and productivity could shape soil microbial communities by supplying different quality resources for microbial growth (Lladó et al., 2018; Tian et al., 2013; Zhao et al., 2017).

Interestingly, we found that plant functional traits and soil variables cooperatively explained much more variation in the soil microbial community than plant functional traits or soil properties alone

(Fig. 2). Together with the significant linkage between CWMs and soil proper-ties, this result indicates that changes in soil microbial community composition and function can be both the direct effects of the CWM and the indirect effects due to changes in soil properties. Of the direct ef-fects, the input and accumulation of diverse litter from plants with different functional attributes supply complex carbon sources to soil microbes (Liu et al., 2010; Zak et al., 1994). Of the indirect effects, changes in soil properties (especially SWC and SOC) induced by CWMs simultaneously play a crucial role in the shaping of soil microbial community.

4.3. Relationships between soil properties and community-weighted mean traits

In our study, we found that the CWMs were strongly associated with soil physicochemical properties (Table 2). These results support the mass ratio hypothesis and suggest that soil properties are primarily determined by the functional traits of dominant species. Consistent with our results, many studies have reported that dominant plant traits ex-plain the changes in soil ecosystem functions. For example, Garnier et al. (2004) proposed that functional markers such as SLA, LDMC, and LNC can be used to assess the impacts of community changes on aboveground net primary productivity, litter decomposition, and SOC. In our study, the fast-growth plant species that produce a high quality litter with higher SLA, LNC, LPC, and lower LDMC in SL and CF are typically replaced by slow-growth species producing litter with the opposite characteristics in NSF and SNF (Orwin et al., 2010). Therefore, the higher SOC in NSF and SNF is probably due to two reasons: i) an increase in the rate of litter input and community standing biomass, and ii) a decrease in the rate of litter decomposition. The accumulation of SOC subsequently induced changes in soil TN and TP. We therefore conclude that changes in soil properties across land restoration types primarily contribute to the enhancement of plant productivity and litter biomass due to changes in plant community structure and the re-placement by dominant plant species with different functional traits.

5. Conclusions

363

364 Our results suggest that soil microbial community structure and carbon-metabolic functions
365 significantly differed among land restoration types. The significant relationships among the soil
366 microbial community, CWMs, and some soil properties suggest that soil microbial community
367 structure and carbon-metabolic functions could be shaped by the functional traits of different
368 dominant plant species and soil properties caused by CWMs. Meanwhile, variance partitioning
369 revealed that plant functional traits and soil variables cooperatively explained 67% and 64%
370 variation in soil microbial community structure and carbon-metabolic functions. Meanwhile, our
371 results imply that natural recovery of forests (NSF and SNF) were better than man-made plantation
372 and secondary shrubland in determining soil microbial communities and further developing soil
373 quality.

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379 Declaration of Competing Interest

380 The authors declare that they have no known competing financial interests or personal relationships
381 that could have appeared to influence the work reported in this paper.

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Table 1 Plant community attributes and soil physicochemical properties in four land restoration types.

	SL	CF	SNF	NSF	F value
Species diversity indices					
Shannon index	1.85 ± 0.05 a	1.13 ± 0.12 c	1.75 ± 0.11 ab	1.57 ± 0.17 b	10.11
Richness	11.40 ± 0.56 a	10.20 ± 1.32 a	10.80 ± 1.11 a	10.60 ± 1.03 a	0.78
Evenness	0.77 ± 0.02 a	0.49 ± 0.05 c	0.75 ± 0.04 ab	0.65 ± 0.06 b	9.34
Functional diversity indices					
CWM-LDMC	285.7 ± 3.7 c	322.4 ± 7.3 b	395.8 ± 13.6 a	406.8 ± 11.9 a	53.67
CWM-SLA	13.25 ± 0.24 b	17.47 ± 0.58 a	11.32 ± 0.61 c	9.71 ± 0.06 d	61.66
CWM-LNC	14.02 ± 0.18 a	8.90 ± 0.17 b	8.74 ± 0.14 b	9.22 ± 0.10 b	254.62
CWM-LPC	0.47 ± 0.01 a	0.30 ± 0.01 b	0.28 ± 0.01 b	0.27 ± 0.01 b	122.20
CWM-SRL	38.90 ± 0.69 b	44.02 ± 1.12 a	29.26 ± 1.35 c	18.91 ± 0.72 d	122.15
Soil physicochemical properties					
pH	4.15 ± 0.14 a	4.08 ± 0.04 a	4.26 ± 0.01 a	4.19 ± 0.11 a	0.70
SWC (%)	26.34 ± 0.48 b	29.07 ± 1.59 b	31.98 ± 2.37 ab	37.11 ± 2.60 a	5.61
SOC (mg/g)	28.42 ± 1.41 b	26.02 ± 1.78 b	38.62 ± 3.38 ab	45.11 ± 7.70 a	4.19
TN (mg/g)	0.48 ± 0.05 b	0.44 ± 0.05 b	0.47 ± 0.05 b	0.69 ± 0.06 a	6.51
TP (mg/g)	0.25 ± 0.00 b	0.23 ± 0.01 b	0.22 ± 0.02 b	0.34 ± 0.05 a	4.33

Values are mean ± standard error. Different letters indicate significant differences among land restoration types based on the LSD test ($P < .05$). *Significant difference between plant communities based on a one-way ANOVA (* $P < .05$ and ** $P < .01$). SL, shrubland; CF, coniferous forest; SNF, semi-natural forest; NSF, natural secondary forest. CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.

Table 2. Correlations between plant community attributes and soil physicochemical properties.

	pH	SWC	SOC	TN	TP
CWM-LDMC	0.24	0.76	0.65	0.19	0.24
CWM-SLA	−0.35	−0.57	−0.65	−0.50	−0.45
CWM-LNC	−0.10	−0.53	−0.32	−0.01	−0.01
CWM-LPC	−0.08	−0.69	−0.44	−0.18	−0.15
CWM-SRL	−0.34	−0.73	−0.74	−0.63	−0.58

Asterisks indicate the significance of correlation ($P < .05$ and $P < .01$). CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.

Table 3. Soil microbial community composition and community-level physiological profiles in four land restoration types.

	SL	CF	SNF	NSF	F values
Soil microbial community composition					
Total Biomass (nmol/g)	11.94 ± 0.06 b	14.08 ± 0.08 b	21.09 ± 1.55 a	23.90 ± 1.24 a	32.58
Bacteria (nmol/g)	6.33 ± 0.10 b	7.92 ± 0.06 b	12.04 ± 0.95 a	13.68 ± 0.70 a	33.83
Fungi (nmol/g)	1.89 ± 0.06 b	2.03 ± 0.06 b	3.10 ± 0.16 a	3.30 ± 0.29 a	17.56
Actinomycetes (nmol/g)	1.00 ± 0.02 c	1.33 ± 0.04 bc	1.63 ± 0.18 ab	1.93 ± 0.11 a	13.68
AMF (nmol/g)	0.26 ± 0.00 c	0.31 ± 0.01 c	0.47 ± 0.04 b	0.56 ± 0.02 a	43.73
Protozoa (nmol/g)	0.04 ± 0.00 b	0.03 ± 0.00 b	0.08 ± 0.01 ab	0.13 ± 0.04 a	5.39
G+ (nmol/g)	2.30 ± 0.05 b	2.73 ± 0.05 b	3.72 ± 0.32 a	4.27 ± 0.25 a	19.03
G- (nmol/g)	3.21 ± 0.12 c	4.34 ± 0.01 b	7.18 ± 0.55 a	8.27 ± 0.39 a	47.16
Fungi/Bacteria	0.30 ± 0.01 b	0.26 ± 0.01 ab	0.26 ± 0.01 ab	0.24 ± 0.02 a	3.11
G+/G-	0.72 ± 0.04 a	0.63 ± 0.01 b	0.52 ± 0.00 c	0.52 ± 0.02 c	22.03
Community-level physiological profiles					
AWCD	0.37 ± 0.13 bc	0.22 ± 0.03 c	0.67 ± 0.07 a	0.60 ± 0.08 ab	5.89
Carboxylic acids	0.50 ± 0.04 b	0.28 ± 0.04 c	0.81 ± 0.09 a	0.52 ± 0.06 b	13.01
Polymers	0.49 ± 0.12 b	0.61 ± 0.07 b	0.73 ± 0.06 ab	0.90 ± 0.04 a	4.97
Carbohydrates	0.42 ± 0.10 bc	0.21 ± 0.03 c	0.64 ± 0.07 ab	0.72 ± 0.10 a	8.90
Phenolic acids	0.18 ± 0.09 b	0.14 ± 0.09 b	0.46 ± 0.16 a	0.65 ± 0.03 a	5.71
Amino acids	0.22 ± 0.06 b	0.20 ± 0.04 b	0.58 ± 0.06 a	0.73 ± 0.16 a	8.43
Amines	0.20 ± 0.10 a	0.15 ± 0.04 a	0.20 ± 0.07 a	0.37 ± 0.15 a	0.99

Values are mean ± standard error. Different letters indicate significant differences among land restoration types based on the LSD test ($P < .05$). Significant difference between plant communities based on a one-way ANOVA ($P < .05$ and $P < .01$). SL, shrubland; CF, coniferous forest; SNF, semi

Table 4. Significance analysis of correlation between the redundancy analysis (RDA) axes of microbial community properties (PLFA and CLPP) and indices of species diversity, functional traits, and soil properties.

Variables	PLFA				CLPP			
	RDA1	RDA2	r ²	P	RDA1	RDA2	r ²	P
Species diversity indices								
Shannon index	0.054	−0.999	0.362	0.136	−0.467	0.884	0.397	0.100
Richness	0.824	−0.567	0.438	0.077	−0.841	0.541	0.554	0.026
Evenness	−0.299	−0.954	0.282	0.213	−0.200	0.980	0.211	0.351
Functional diversity indices								
CWM-LDMC	0.998	0.015	0.758	0.002	−0.996	0.089	0.544	0.034
CWM-SLA	−0.764	0.645	0.833	0.001	0.992	−0.126	0.677	0.006
CWM-LNC	−0.737	−0.676	0.731	0.002	0.797	0.604	0.223	0.300
CWM-LPC	−0.854	−0.520	0.763	0.002	0.859	0.511	0.336	0.178
CWM-SRL	−0.908	0.419	0.899	0.001	0.983	0.183	0.809	0.001
Soil physicochemical properties								
pH	0.950	−0.313	0.129	0.519	−0.987	0.161	0.216	0.330
SWC	0.986	0.168	0.742	0.006	−0.884	−0.467	0.297	0.223
SOC	0.999	0.044	0.715	0.005	−0.946	−0.323	0.271	0.264
TN	0.736	−0.677	0.422	0.096	−0.726	−0.688	0.419	0.091
TP	0.994	−0.105	0.299	0.216	−0.425	−0.905	0.324	0.172

r² represents the proportion of variance explained. Asterisks indicate the significance of correlation based on Monte Carlo permutation test (n = 999). P < .05, P < .01, P < .001. CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.

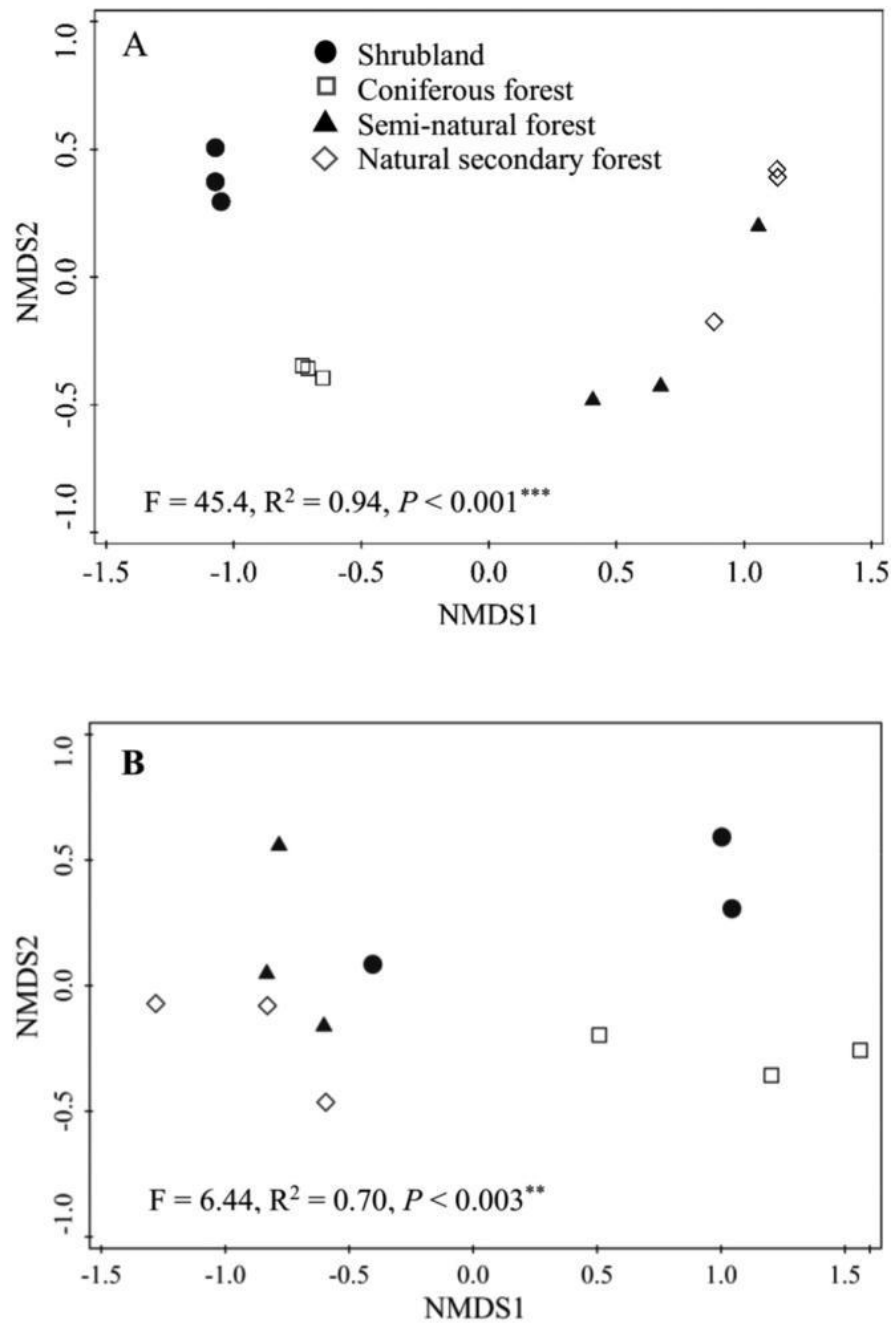


Fig. 1. Non-metric multidimensional scaling (NMDs) analysis of (A) soil mi-crobal community composition and (B) soil microbial carbon-metabolic functions within soils across land restoration types (the distance metric was the Bray-Curtis metric). The same shapes represent three replicates of the twelve plots of this study. The significance test was based on a PERMANOVA.